

THE KRAMERIACEAE IN THE SOUTHEASTERN UNITED STATES¹

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KRAMERIACEAE Dumortier, Anal. Fam. 20, 23. 1829, nom. cons.

(RATANY FAMILY)

A distinctive monogeneric family, mostly of arid regions in the New World. The family is characterized by shrubby or herbaceous perennial habit; exstipulate, simple and entire or rarely trifoliolate leaves; irregular flowers; petaloid calyx that much exceeds the dimorphic petals; stamens confined to the adaxial part of the flowers; apically dehiscent anthers; bicarpellate gynoecium with one fertile and one sterile carpel; and spiny, one-seeded, indehiscent fruits. TYPE GENUS: *Krameria* L.

Krameria is a quite singular genus, and its phyletic placement is problematical. It has been treated by various authors as the sole member of Krameriaceae, of the Polygalales; as tribe Kramerieae, of the Polygalaceae; as Krameriaceae, of the Rosales; as subfamily Kramerioideae, of the Leguminosae; and as tribe Kramerieae, subfamily Caesalpinioideae, of the Leguminosae. The structure of the wood, the exstipulate leaves, the vascular anatomy of the pedicel and receptacle, and the number and size of the chromosomes, as well as the frequency of chromosomal chiasmata, definitely indicate that *Krameria* is not closely allied to Leguminosae. Comparative information on Polygalaceae is mostly lacking, but three- or four-colporate pollen, adaxial stamens, collateral ovules, and seeds with endosperm are features never or seldom found in that family. Until more is known of *Krameria* and its supposed relatives, it seems best to keep the genus in its own family of uncertain affinities.

1. *Krameria* Linnaeus in Loeffling, Iter Hisp. 195. 1758.

Perennial herbs [or, more often, low, much-branched, spinescent shrubs] from thick crowns on woody rootstocks; root system of long, few-branched taproots and/or horizontal lateral roots [some species root parasites];

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plants often densely pubescent with simple [and glandular] trichomes. Leaves small, alternate, simple and entire [or rarely trifoliolate], sessile [or shortly petiolate]; stipules absent. Inflorescences axillary, 1-flowered [or, by condensation of the distal internodes, of terminal racemose clusters], the pedicels with 2 opposite, foliaceous bracts, both pedicels and bracts persistent after the fruits have fallen. Flowers perfect, irregular, resupinate or not, the perianth red-purple [or yellow]. Sepals 5 [4], quincuncially imbricate in aestivation, petaloid, much larger than petals, slightly unequal, the abaxial one somewhat gibbous, all deciduous. Petals 5 [4], dimorphic, the 3 adaxial ones long clawed, the claws connate [or free], the blades small, orbicular [or absent] the 2 abaxial petals sessile, thick, fleshy, glandlike. Androecium of 4 [3, 5] stamens in 2 unequal pairs opposite the 3 adaxial petals, a fifth, sterile stamen rarely found on the opposite side of the flower; filaments thick, basally connate [or distinct] and free or partly adnate to the claws of the adaxial petals; anthers narrowly conical, basifixed, opening by apical pores or slits; pollen 3- or 4-colporate, oblate-spheroidal, the sexine bacculate and striate. Gynoecium superior, syncarpous, of 1 fertile and 1 sterile carpel, the fertile carpel with 2 collateral anatropous ovules, pendulous from an adaxial placenta near the top of the locule; style obliquely terminal; stigma terminal, punctiform. Fruit dry, pubescent [or glabrous], nearly globose to ovoid, indehiscent, covered with long spines, 1-seeded; seeds without endosperm, the seed coat smooth, membranaceous; embryo straight, the cotyledons thick and fleshy, planoconvex, basally sagittate, the radicle superior. Base chromosome number 6. TYPE SPECIES: *K. Ixine* L.; see Linnaeus, Syst. Nat. ed. 10. 899. 1759. (Dedicated to Johann Georg Heinrich Kramer, an 18th Century Austrian botanist.) — RATANY, RHATANY.

Twenty or more species of xerophytes in four largely disjunct regions: *Krameria Ixine* in the West Indies from Hispaniola to Grenada, in northern South America, and perhaps in Paraguay; possibly 15 species in deserts of southwestern North America from California and Texas to Honduras; about four species in cordilleran South America from Peru to northern Chile and Argentina; and perhaps no more than six species in eastern Brazil. *Krameria lanceolata* Torrey occurs in the southern United States and adjacent Mexico. The genus has been revised only regionally, and the relationships between species occurring in the different geographical areas are difficult to determine.

Krameria lanceolata (*K. spathulata* Small in Britton), $2n = 12$, one of the most widely distributed species of the genus, occurs from mid-peninsular Florida to Georgia, and apparently disjunctly in Arkansas, Oklahoma, southern Kansas, Texas, southeasternmost Colorado, southeastern Arizona, Chihuahua, and Coahuila. It is found most commonly in open rocky or sandy areas. It is easily distinguished by its prostrate or trailing herbaceous stems; canescent linear leaves; bright wine-colored, irregular, solitary flowers with petaloid sepals and dimorphic petals (the adaxial three with long claws, the abaxial two glandlike); paired sta-

mens with thick, basally united filaments and tapering anthers that dehisce apically; and echinate, indehiscent fruits. Some plants of this species from northern Mexico have yellow flowers; whether these are merely a color form or a taxon worthy of recognition remains to be seen. The name *Krameria secundiflora* DC., based on a Sessé & Mociño drawing and sometimes applied to this species, should be rejected as an ambiguous name.

Meiotic chromosomes of the species of *Krameria* that have been examined cytologically are among the largest known from the dicotyledons, perhaps exceeded only by some species of *Paeonia* (Ranunculaceae) and of *Phoradendron* and *Psittacanthus* (Loranthaceae). At anaphase I, the longest chromosome of *K. lanceolata*, as observed by Lewis, *et al.*, measured 24.6 μm ., the shortest was 10 μm ., and the average length of the six was 17.3 μm .

Some species of *Krameria*, while outwardly appearing to be completely autotrophic, are partly parasitic on the root systems of other species. *Krameria Grayi* Rose & Painter (*K. canescens* Gray, non Willd.), white ratany, $2n = 12$, has been found parasitizing species of *Acacia*, *Ambrosia*, *Encelia*, *Ephedra*, *Larrea*, *Lycium*, *Menodora*, *Parkinsonia*, *Prosopis*, and *Ziziphus*. Seedlings of *K. Grayi* can be independent for an undetermined period of time but soon become attached to roots of host species if they are growing in association with them. In contrast to most desert perennials, which have either deep taproots or specialized water-storage organs, the roots of *K. Grayi* are usually thin and largely superficial (although Kuijt has illustrated a plant of this species with a long taproot). *Krameria parvijolia* Bentham, range ratany, and *K. paucifolia* (Rose) Rose also are reported to be root parasites.

Flowers of *Krameria* species are papilionaceous in appearance and seemingly adapted for entomophily, although there have been no reports on specific pollinators. It is difficult to determine floral orientation on herbarium specimens, but populations of some species, including *K. lanceolata*, have resupinate flowers. The intraspecific constancy of this feature and its effect on pollination are not known. The fruits of *K. lanceolata* have spines that are pubescent below with small bumps or barbs toward the apices; some other species have one to numerous retrorse barbs above or four large barbs at the tips of the spines. The fruits probably are dispersed by fur-bearing animals. Kuijt observed that many fully formed fruits of *K. Grayi* are empty; the same condition seems to be fairly common in *K. lanceolata*. A case of vivipary was seen by Palmer in *K. Grayi* (see Vasey & Rose). Kuijt's observation that the fleshy petals enlarge with the fruit and eventually surround it could not be substantiated from herbarium specimens, which suggest instead that the petals are promptly deciduous in most species.

According to Bentham's unique interpretation of the flower, the calyx is composed of the four large sepals, the abaxial, gibbous sepal representing a connate pair. The fifth, small "sepal," which is sometimes absent, represents the corolla. The three clawed "petals" and the two lateral

stamens comprise the outer androecial whorl, while the two upper stamens and the two fleshy "petals" form the inner staminal series. While this most interesting theory would support an alliance of *Krameria* with Polygalaceae, more recent studies have shown it to be incorrect. Milby, however, found that each of the adaxial, clawed petals of *K. lanceolata* has a single vascular trace (as in the stamens) while the abaxial, glandlike petals have several veins. Milby's study showing that the gynoecium of *Krameria* has a fertile carpel and a sterile one reaffirms Baillon's frequently overlooked observation (1873) that the ovary initially has two locules, one of which does not develop.

The dried roots of *Krameria triandra* Ruiz & Pavon, Peruvian ratany; *K. argentea* Martius, Para or Brazilian ratany; *K. tomentosa* Saint-Hilaire, Savanilla ratany; and *K. Ixine* contain a powerful astringent, and these species have been listed in pharmacopoeias as useful in the treatment of various conditions, such as diarrhea, hemorrhages, tumors, and sores. The roots of these species contain a high concentration of tannin, and they have been used in tanning of leather. *Krameria triandra* has also been used as a tooth powder and as an additive to port wine. The Indians of the American Southwest used infusions of twigs of *K. parvifolia* for the treatment of eye sores, and they obtained red, brown, and yellow dyes from the stems and roots of this species. *Krameria parvifolia* and *K. Grayi* are favorite browse plants of range animals.

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